Forest Ecology and Management 468 (2020) 118180

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Plant traits as indicators of recovery of reclaimed wellsites in forested areas: Slow but directional succession trajectory

Ermias T. Azeria[a,*], Kierann Santala[b], Anne C.S. McIntosh[c], Isabelle Aubin[b]

[a] Alberta Biodiversity Monitoring Institute, University of Alberta, Edmonton, AB T6G 2E9, Canada
[b] Natural Resources Canada, Great Lakes Forestry Centre, Sault Ste. Marie, ON P6A 2E5, Canada
[c] Augustana Campus, University of Alberta, Camrose, Alberta T4V 2R3, Canada

ARTICLE INFO

Keywords:
Community assembly
Ecological recovery
Environmental filtering
Functional trait
Post-disturbance succession
Land reclamation
Severe disturbance

ABSTRACT

Trait-based approaches can provide a generalizable mechanistic understanding of complex post-disturbance succession dynamics of plant communities. Much of our knowledge regarding successional trajectories of functional trait composition come from observations of natural disturbances that leave physical and biological legacy on site for self regeneration. We lack, however, understanding of the long-term recovery in severely degraded lands following reclamation through active revegetation. To address this gap, we examined changes in trait composition of forest understory plant communities in reclaimed oil and gas wellsites using chronosequence data (7–48 years since reclamation) to assess recovery towards that of post-harvest and natural post-fire reference forest sites. We used multiple traits associated with resource acquisition (e.g., fast growth) and performance ability metrics (e.g., shade-tolerance) with putative environmental factors to evaluate the trait-environment relationships underlying plant community recovery in reclaimed sites. We found an overall directional change in functional composition with time since reclamation towards that observed in reference sites, but even older reclaimed sites remained significantly different from reference sites. This could be related to differential trajectory patterns among traits where some trait values progressed towards those of reference (long-distance dispersal by wind decreased with time since reclamation) whereas some fast-resource acquisition traits and exotic species showed no change and remained dominant in older reclaimed sites. The strong link between traits and environment suggests a significant influence of time and subsequent developing site conditions (e.g., canopy cover) as well as enduring legacies of wellsite operation/reclamation (e.g., high soil bulk density and exotic species) on functional composition. Knowledge of functional composition trajectories in severely degraded ecosystems, such as wellsites, could improve our understanding of recovery processes and inform more effective reclamation practices by identifying putative underlying environmental factors and specific ecological attributes that may delay successful recovery.

1. Introduction

The investigation of ecological succession, i.e., how the plant community changes over time following natural and anthropogenic disturbances, and the underlying biotic and abiotic factors has been a long standing pursuit of ecology (Connell and Slatyer, 1977; Pickett et al., 1987; Drake, 1990; Azeria et al., 2011; Meiners et al., 2015). Understanding these underlying factors and the processes that drive succession also has practical implications in restoration and reclamation practices (Aide et al., 2000; Young et al., 2005), including assessing recovery of degraded ecosystems (Young et al., 2005) and developing better restoration/reclamation practices to restore/reclaim natural ecosystems (Lohbeck et al., 2017). Much of this understanding has been generated by studying changes in species composition and richness (Wortley et al., 2013). However, in recent years, there has been an increasing emphasis on using information beyond species identity to also consider functional attributes of ecological communities as a basis to assess successional trajectories (Meiners et al., 2015) and restoration targets (D'Astous et al., 2013; Laughlin, 2014). Trait-based assessments can provide a generalizable and integrated indicator of ecological status (Gondard et al., 2003; McGill et al., 2006; Violle et al., 2007) and can be indicative of ecosystem functioning (Lavorel and Garnier, 2002; Diaz et al., 2004; de Bello et al., 2010; also see Funk et al., 2017).

Studies of succession following natural disturbances have revealed general changes in community functional traits (Kumordzi et al., 2015) and convergence towards pre-disturbance condition (Turner et al.,

* Corresponding author.
E-mail address: azeria@ualberta.ca (E.T. Azeria).

https://doi.org/10.1016/j.foreco.2020.118180
Received 14 August 2019; Received in revised form 21 April 2020; Accepted 23 April 2020
Available online 06 May 2020
0378-1127/

1998; Roberts, 2004; Hart and Chen, 2006). The early-successional stage is generally dominated by species that possess a core set of traits (i.e., syndrome) such as fast growth, short life span, abundant seed production and light-demanding (i.e., shade intolerant) (e.g., Huston and Smith, 1987). These traits can be collectively referred to as fast-resource acquisition traits. This trait syndrome is best suited to early post-disturbance conditions when nutrient and light availability is high (Reich, 2014). In later successional stages, assemblages become increasingly dominated by slower growing species with longer life spans, extensive root systems, production of a few large seeds and shade tolerance (Grime, 1977; Grime et al., 1997; Reich, 2014). This trait syndrome enhances resource conservation or resource-use efficiency and competitive ability. Such a deterministic view of succession assumes that environmental filtering acts upon the various traits available in the regional species pool and selects species with ecological traits that confer fitness within a given environmental condition (Connell and Slatyer, 1977; Díaz et al., 1998; Keddy, 1992; Kraft et al., 2015; Weiher and Keddy, 1999), which is implied from trait-environment relationships (Naeem et al., 2012; Thuiller et al., 2006). Successional dynamics are obviously much more complex processes than presented here, as they are also influenced by interspecific interactions among diverse plant communities (Connell and Slatyer, 1977; Pickett et al., 1987; Azeria et al., 2011), stochastic processes such as dispersal limitation (Hubbell, 2001), local site factors such as land-use history (Young et al., 2005), and order of species arrival or priority effects (Fukami et al., 2005; Kardol et al., 2013). These various drivers can have long-term impacts on community assembly and can cause deviations in directional successional trajectories. Understanding the long-term trajectory of functional traits may provide critical information for understanding the relative role of deterministic and stochastic influences on successional pathways.

Despite increasing attention paid to trait-based approaches in naturally-disturbed ecosystems, the nature of successional changes in functional composition of severely degraded and reclaimed ecosystems remains poorly understood. Severe anthropogenic disturbances, such as oil and gas well pad drilling, that completely remove topsoil and vegetation, leave almost no biological legacy for self-recovery to pre-disturbance state. Therefore, vegetation recovery of such severely degraded sites to pre-disturbance condition may be very slow without active reclamation (Chazdon, 2008; Macdonald et al., 2012). This is in contrast to succession after natural disturbance where community reassembly is initiated by native biological legacies (i.e., propagules) left after natural disturbances, which may also be a contributing factor to a directional change towards pre-disturbance state (Turner et al., 1998; Roberts, 2004; Hart and Chen, 2006). Successional patterns typically observed after natural disturbances may or may not apply to highly degraded landscapes. Very few studies have assessed functional recovery of such systems and evaluated whether broad successional patterns exist akin to those after natural disturbances. Thus, there is an important need to understand patterns of functional trait recovery and underlying processes in severely disturbed sites, given the impacts severe industrial disturbances have on natural ecosystems and the various biodiversity components they support (Dhar et al., 2018; Lupardus et al., 2020).

In the boreal forest ecozone of Alberta, Canada, industrial oil and gas disturbance has resulted in more than 239,000 drilled wellsites, of which ~24% have been reclaimed certified or were exempted (Alberta Energy Regulator, 2019). In these industrially disturbed lands, the forest understory vegetation and underlying soils containing plant propagules and seeds have been removed, resulting in the loss of important components of the forest biological legacy. This has created a mosaic of degraded lands that have either undergone or will require active reclamation. Given that the forest understory vegetation contributes significantly to forest biodiversity and a range of forest ecosystem functions (Roberts, 2004; Hart and Chen, 2006), re-establishing a viable forest understory community is an essential part of reclamation in forested areas. However, due to limited availability of native seed propagules from nurseries or natural sources, active conservation and reclamation activities in this region historically used commercially-available, often non-native agronomic grasses and forbs (Alberta Energy and Natural Resources, 1984; Government of Alberta, 1995; Chazdon, 2008; Macdonald et al., 2012; Powter et al., 2012). Rather than focusing on reestablishment of trees on forested lands, the short-term goal of revegetation was to initiate a quick re-establishment of vegetation cover, which is critical for soil stabilization, minimizing the spread of weedy species and promotes nutrient cycling recovery (Remaury et al., 2018; Schuster et al., 2018). The long-term goal of reclamation of Alberta's wellsites is to return the disturbed land to "equivalent land capability" (ELC), i.e., the ability of the land to support biodiversity and various land uses is similar to what existed prior to exploitation activities (Alberta Environment, 2010; ESRD, 2013), which remains poorly understood (Dhar et al., 2018). The few existing long-term studies indicate that plant community composition and structure in reclaimed sites remain different from that of natural ecosystems even after decades (e.g., Pinno and Hawkes, 2015; Lupardus et al., 2019). Persistence of novel abiotic (soil physico-chemical properties) and biotic (non-native crops used in revegetation) factors are commonly implicated to inhibit establishment of native vegetation in reclaimed sites (Zipper et al., 2011; Franklin et al., 2012; Bauman et al., 2015). To our knowledge, there are very few, if any, long-term studies focused on the functional aspect of community recovery in highly degraded systems. Considering the expected slow ecological recovery of wellsites, a long-term chronosequence is necessary to assess if reclaimed sites converge over time towards successional stages typical of naturally disturbed sites (e.g., recovery after fire) or alternatively, other desired land use practices (e.g., recovery after timber harvest).

In this study, we examined the successional trajectory of reclaimed wellsites in forested ecosystems along a post-reclamation chronosequence (7–48 years post certification) to evaluate ecological recovery of plant community traits. Understory vegetation responds rapidly to prevailing proximate ecological conditions (Hart and Chen, 2006; Azeria et al., 2011), thus it can provide a good indication of status of ecosystem ecological recovery on the whole. We assessed ecological recovery by comparing trait composition of reclaimed wellsites along the chronosequence with reference sites grouped into three site types: natural forests (young and mature forests regenerating post fire; here after called natural forests) and young harvested forests ('cut blocks'). This study design allowed us to assess the recovery of reclaimed wellsites not only against naturally-regenerating forests typically used as a target for ecological restoration/reclamation but also against potential alternative lower magnitude disturbance land use (productive harvest) that the reclaimed wellsites may develop into within forestry-managed areas. Our primary objectives were to: (1) determine the magnitude of difference in trait composition of young and old reclaimed wellsites compared to natural forests (young and old) and young harvested forests; (2) determine if the post-reclamation changes of understory communities functional (individual and combined) traits on wellsites follow a directional trajectory rather than a stochastic one; and (3) evaluate the relationship between functional traits and environmental variables (e.g., bulk density, canopy cover). Understanding the complex relationships between functional traits and environmental variables over reclamation recovery period can have important implications for restoration and reclamation practices, including the identification of native species with traits matching the environmental condition (e.g., Martínez-Garza et al., 2013) or potential best practices to improve environmental site conditions and enhance the establishment of species with more desirable trait values (e.g., Lohbeck et al., 2017).

2. Materials and methods

2.1. Study area

The study sites were located in the Central Mixedwood and Lower Foothills Natural Subregions in central Alberta (subregions within Alberta's Boreal and Foothill Natural Regions that are dominated by forest; The Natural Regions Committee, 2006) (Appendix Fig. S1).

The latitude of study sites ranged from 54°12′-56°22′ (N) and longitude ranged from 110°39′-118°7′ (W). The region has short, moderately moist (> 470 mm) warm summers (~15 °C) and long, cold winters (< -13 °C) with abundant snowfall (The Natural Regions Committee, 2006). The landscape in the study area is comprised of deciduous, coniferous and mixedwood upland forests with extensive wetlands. The dominant deciduous species in upland forests include trembling aspen (*Populus tremuloides* [Michx.]) and balsam poplar (*Populus balsamifera* L.), while the most common conifer species include white spruce (*Picea glauca* [Moench]), lodgepole pine (*Pinus contorta* Dougl.), and jack pine (*Pinus banksiana* [Lamb.]). The wetlands are dominated by black spruce (*Picea mariana* [Mill.]), shrub or sedge fens. Typical soils are moderately fine textured Gray Luvisols and gleyed subgroups (The Natural Regions Committee, 2006).

In this study a total of 89 ~ 1 ha area sites were sampled, including 30 wellsites and adjacent natural forest or harvested reference sites and 29 non-adjacent reference harvested sites. The 30 reclaimed wellsites that were selected ranged in age from 7 to 48 years after reclamation certification (mean of 20 years). The sites were selected from a larger pool of well sites that met study requirements: i.e., all certified reclaimed wellsites were located in upland forest types (deciduous, coniferous, or mixedwood), without active wellsite directly adjacent, public land, within ~1.5 h of Slave Lake or Fox Creek field bases, accessible on foot (maximum ~1km from nearest road). Detailed information on the criteria that were used to approve reclamation certificates are provided in Government of Alberta, 1995 and AESRD, 2013. Information on some of the types of seed mixes that would have likely been used historically for revegetation are found in Alberta Energy and Natural Resources, 1984 (Appendix B) and Hardy BBT Ltd. (1989). As historical records of reclamation activities conducted on each wellsite are not available, we were unable to evaluate differences in the specifics of reclamation efforts (e.g., reseeding methods, seed source, herbicide treatment, etc.) for individual sites.

We sampled 30 (~1 ha) reference sites that were located directly adjacent to the wellsites. The reference sites were intended to capture the types of plant communities to which the reclaimed, previously disturbed area would ideally return over time, and thus provided a parameter to measure the trajectory of community recovery (Purcell et al., 2002). Their placement around the wellsites ensured exposure of the wellsites and reference sites to similar historic natural environmental conditions and disturbances. Because we wanted to compare the wellsite recovery against post-harvest disturbance that would results from an alternative land use (there were few deciduous-dominated young clear-cut forests in the adjacent reference sites), we also included data from an additional 29 conventional harvested reference sites (10–20 year cut blocks) within the same study region. These additional harvested reference sites are part of the database maintained by the Alberta Biodiversity Monitoring Institute (ABMI) core monitoring program (ABMI, 2010; www.abmi.ca). The additional criteria used for selecting the harvested sites was that the whole 1 ha should be harvested (most ABMI sites include a mix of natural and harvested areas), and deciduous-dominated. The young harvested sites were in aspen-dominated upland forests harvested ~15 years old prior to vegetation survey with 2% merchantable volume left and their stand structure and plant species groups at time of survey was similar to those found in areas 20–40 years or > 40 year post-fire (Huggard et al., 2015).

2.2. Understory vegetation data

Field sampling of vascular plant composition (excluding overstory tree species) was carried out by trained technicians in summer of 2014 in the 30 wellsite and adjacent reference site pairs. Data collection followed protocols established in McIntosh et al., (2019). To briefly summarize plant sampling, occurrence of plant species was recorded within each ~100 × 100 m (1 ha) wellsite, which was divided into four ~50 × 50 m quadrants. In a few cases, the quadrants were slightly smaller where the area cleared for wellsite construction was smaller than 1 ha. After an initial 10 min creating a species list with names of vascular plants observed at the study site, each quadrant was surveyed for 20 min for a total of 80 min per wellsite (McIntosh et al., 2019, Fig. 8) regardless of well site size and so were considered to be equivalent in terms of vascular plant sampling effort. Occurrence of vascular plant species was recorded in each quadrant. The number of occurrences across quadrants was summed for each species per site (0–4) and used as our metric of species relative abundance. Similarly, four reference 50 × 50 m quadrants were laid out beginning at the edge of each corner of the wellsite (see McIntosh et al., 2019, Fig. 8), within the nearby "undisturbed" forested landscape to sample species relative abundance. When placing reference quadrants, the exact locations were adjusted as necessary to avoid areas impacted by any type of human disturbance (e.g., roads, pipelines).

The 29 young harvested reference sites were surveyed in summers between 2010 and 2012 using the same floristic inventory protocol (ABMI, 2010), except that instead of a paired 1 ha wellsite and 1 ha of reference, there was only a single 1 ha (100 × 100 m) plot within each harvested site that was sampled. Vascular plants were identified to the species level in the field and voucher specimens by plant taxonomists at the Alberta Biodiversity Monitoring Institute. When this was not possible, plants were identified to genus or another lower taxonomic resolution level, e.g., some species in the genera *Carex* and *Salix* were analyzed at that level.

2.3. Plant traits and characteristics

We evaluated ten plant traits and metrics that are considered to influence plant colonization ability and performance (i.e., dispersal, establishment and persistence) (Table 1). More specifically we distinguished between fast-resource acquisition traits typical of early-successional species that colonize quickly (e.g., annuals, abundant seed production), and traits typical of late-successional species, which are linked to resource conservation (e.g., longevity, shade tolerant) (Grime, 1977; Grime et al., 1997; Reich, 2014). We use the term trait in its broader sense and include metrics related to plant morphology and propagation (growth form, lateral extension, maximum height), regeneration and dispersal strategy (seed production, seed dispersal vector, seed weight) and resource utilization (water, light requirements and longevity). We also include species origin status in Alberta (native or exotic) (Table 1). Trait information was compiled from the Traits of Plants in Canada (TOPIC) database (Aubin et al., 2020).

2.4. Environmental data

For each site, we compiled environmental variables reflecting broad landcover types (GIS data) and fine scale (field data) habitat characteristics and soil properties. Each of these components are described below (see McIntosh et al. (2019) for more detail).

2.4.1. GIS-extracted data

We used the detailed wall-to-wall vegetation (version 5; ABMI 2015) and Human Footprint GIS layers (ABMI Human Footprint Inventory for 2012, Version 3) created by ABMI to broadly characterize

Table 1
Plant traits and characteristics compiled from Traits of Plants in Canada (TOPIC) database.

Trait (abbreviation)	Variable type	Trait classes	Code	Description	Species (n)
Growth form (GF)	Nominal	Graminoid	Graminoid	Graminoid	33
		Forb	Forb	Forb	102
		Shrub	Shrub	Shrub	51
		Fern and allies	Fern	Fern	7
Height (HT)	Quantitative	1.1–8.01 (Mean ± sd: 4.44 ± 1.12); log scale			
Lateral extension (LE)	Ordinal (0–4)	Limited	0	No vegetative propagation	24
		Clonal compact	1	Limited horizontal propagation	55
		Clonal extensive (*non- Phanerophyte*)	2	With significant horizontal propagation	93
		Clonal intermediate (*Phanerophyte*)	3	With moderate horizontal propagation	13
		Clonal extensive (*Phanerophyte*)	4	With significant horizontal propagation	8
Seed production (SDPRO)	Nominal	Abundant	a	> 1000/year	114
		Semi-abundant	s	20–1000/y	65
		Few, scarce	f	1–20/y	14
Seed weight (SDWT)	Quantitative	Number of seeds/kg; 7.05–25.33 (Mean ± sd: 15.02 ± 3.53); log scale			
Seed dispersal vector (DI)	Nominal	Animal	a	Animal other than birds (external or internal)	60
		Bird	bi	bird	31
		Uunassisted	g	Unassisted/Water	15
		Low	l	Explosive/insect	9
		Wind far	wf	Long dispersal by wind	53
		Wind short	ws	Short dispersal by wind	25
Water preference (WP)	Ordinal (0–1)	0, 0.2, …,1	Xeric (0) to humid (1)		
Light requirement (LI)	Nominal	Shade intolerant/light demanding	i		75
		Shade mid tolerant	m		76
		Shade tolerant	s		42
Longevity/perennially (PER)	Binary	Short	1	Annual + biannual	18
		Long	2	Perennial	175
Origin status (ST)	Binary	Exotic		Exotic	20
		Native		Native	173

the paired wellsite and reference sites, as well as the harvested reference sites (i.e., the cut-block sites). For the wellsites, landcover information was extracted for a 1 ha square area centered on each site or by intersecting the entire wellsite boundary with the GIS layers for the cases where the site area was < 1 ha. To account for the resulting area differences between wellsites, all the extracted habitat information was expressed as proportions relative to the area sampled. Similarly, representative land cover information of the adjacent reference area was extracted by taking a circular buffer of 0.25 ha centered at each of the four reference quadrants (total 1 ha). For the harvested sites selected from the core ABMI monitoring program, proportion of vegetation and human footprint was extracted within a 1-ha area around the center point of each sampled site.

Based on the extracted GIS data, we classified the wellsites and reference sites into broad site types. As expected, all the wellsites were within cleared areas, although some had a portion of forests from surrounding areas intergrading to the wellsites along the edges. The wellsites differed in time since reclamation and certification (Range: 7 to 48 yrs post-certification; mean = 20 years) and were further classified into two age classes: young reclaimed (Y.Rec = 7–19 years; 18 wellsites) and old reclaimed (O.Rec: 21–48 years; 12 wellsites). All of these sites were reclaimed using the same reclamation criteria (described in the study area section above) thus a chronosequence approach is appropriate to use. Most of the reference sites adjacent to wellsites were dominated by mature forest (M.For = 50–120 years; 17 sites) or young regenerating forest (Y.For= < 20 years; 7 sites) originating from natural forest fires. However, six of the adjacent reference sites were dominated by recently harvested or young cut blocks (Y.Cut = 10–20 years, except for one that was 5 years old) intermingled with forest that originated from fire. All the additional post-harvest sites selected from ABMI core sampling were young cut blocks (Y.Cut = 10–20 years; 29 sites). We used these site groupings (Y.Rec, O.Rec, Y.Cut, Y.For and M.For) as the basis for comparing overall trait similarity of the post-reclamation chronosequence of wellsites with reference sites. We selected the 20-year cut-off because vegetation communities in naturally disturbed sites tend to stabilize after approximately 20 years of age of canopy initiation (Hart and Chen, 2006).

2.4.2. Field-collected data

We considered chemical and physical properties that are indicators of soil quality and important for plant growth (reviewed in Schoenholtz et al., 2000). Five soil variables, namely soil bulk density (BD), pH, electrical conductivity (EC), total nitrogen (N) and total organic carbon (OC) were estimated based on five sample points in each of the quadrants (McIntosh et al., 2019). Soil pH, EC, N and OC were measured at four depths (0–15, 15–30, 30–60 and 60–100 cm), while bulk density was measured at the two uppermost depths (0–15 cm, 15–30 cm). The measurements were highly correlated across soil depths and among soil variables (Appendix Table S1). Thus, we excluded variables that were highly correlated ($|r| > 0.7$, Dormann et al., 2013) and retained six soil properties measured at the shallowest and deepest depths based on their correlation. In addition, the following habitat characteristics were estimated based on field sampling protocols outlined in detail in McIntosh et al. (2019): canopy cover, total basal area (BA), total coarse woody debris (> 7 cm diameter) volume (CWD) and organic soil horizon (LFH: Litter, Fragmented (partially decomposed) litter and Humus) depth. Briefly, all the variables were measured in each quadrant with corresponding specific protocols to each (plot size within quadrants) and they were averaged or summed across quadrants to give site-level information. For example, total basal area was estimated from field measurements taken on all trees (live, dead) that had a minimum of 1.3 m height and measured within three different plot sizes based on tree diameter at breast height (all trees = 5 × 5 m; ≥ 7 cm dbh = 10 × 10 m; ≥ 25 cm dbh = 25 × 25 m plot) nested within each quadrant (Figs. 9, 10 McIntosh et al., 2019). Some of the habitat characteristics were also highly correlated with each other (e.g., canopy cover and BA: r = 0.72) and with soil parameters (e.g., LFH and OC). Highly correlated predictors ($|r| > 0.7$) were excluded from each pair, choosing the variable with stronger ecological meaning for modelling plant distribution in the boreal forest; we kept five predictors to reflect major environmental gradients that we expected to influence the distribution and composition of the studied plant communities: bulk density (surface), pH and OC at the surface (0–15 cm), pH and OC of deeper soil (60–100 cm), CWD and canopy cover. All of these environmental variables were available for the wellsites and adjacent

reference sites, while for the ABMI young harvested reference sites, soil measurements were undertaken only at surface (organic layer and top 5 cm of mineral soil) and there was no measurement of bulk density. Summary statistics of the habitat variables considered are provided in supplementary material (Appendix Table S2).

2.5. Statistical analyses

For each site, we summarized species richness and the total relative abundance for all species (i.e., sum of detections of all species in 4 quadrants per site), and tested for significant difference among site types using one-way analysis of variances (ANOVAs). When there were significant differences (alpha = 0.05), we conducted Tukey HSD post-hoc tests for pairwise comparisons.

We then performed the following analyses to answer our three main research questions. We applied a set of multivariate methods to ascertain whether the identified patterns were robust to the methods used. First, we asked whether there were differences in understory plant traits among the reclaimed sites (Y.Rec and O.Rec) and the natural forest (Y.For and M.For) and harvested (Y.Cut) reference site types. To answer this question, we calculated community-weighted trait means (CWM) for each site by weighting species traits by relative species abundance at each site (Garnier et al., 2004). This measure quantifies the dominant trait values in a community. A Principal Component Analysis (PCA) was performed on CWM to explore differences among site types in multiple trait space and depicted the overall correlation among trait types. To test for differences in overall CWM composition among site types, we performed permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001). Multi-trait functional dissimilarity was calculated between each pair of communities (sites) using a Gower dissimilarity index (Gower, 1971), which is appropriate to deal with variables (here CWM of each trait) measured in different units (Pavoine et al., 2009). We also performed *post-hoc* pairwise comparisons among sites types. We used the false discovery rate (FDR; Benjamini and Hochberg, 1995) on p-values to adjust for multiple testing. Furthermore, we performed a permutational analysis of multivariate homogeneity of group dispersions (PERMDISP; Anderson et al., 2006) to determine if differences in within-group dispersion could have contributed to significant results in PERMANOVA test. Tests of significance of PERMANOVA and PERMDISP were conducted using 9999 permutations (alpha = 0.05).

Second, we asked whether the traits of plant communities in reclaimed wellsites followed a directional change over time since reclamation. We considered the effects of time since reclamation in two ways. First, we determined whether traits of communities in the wellsites were undergoing directional change along our post-reclamation chronosequence and were converging towards similar trait composition to that found in reference communities. Such reference sites provided a parameter to measure the trajectory of community recovery over time (Purcell et al., 2002). We emphasized comparison of the wellsite trajectories against multiple sites, thus taking into consideration the natural variation that can occur among the reference sites (Hobbs and Norton, 1996; Ruiz-Jaen and Aide, 2005) and recognized the dynamic nature of the putative reference sites (Hiers et al., 2012). In this case, we first calculated the mean trait similarity (i.e., 1-Gower dissimilarity) of each wellsite to each of the reference site types (Y.For, M.For and Y.Cut) and then evaluated the relationship between trait similarity and time since reclamation. We used an analysis of variance (ANOVA) to determine if slopes were significantly different from zero (alpha = 0.05). In addition, we compared differences in intercept and slopes of convergence towards different site types using generalised least square models (GLS), which accommodate for variation in residuals among response variables, in this case mean similarity to the different site types. We then evaluated directional change among the wellsites using a time-lag regression analysis (Collins et al., 2000), where the dissimilarity or divergence in functional trait composition between pairs of wellsites was regressed against each difference in time since certification. This approach has been used to estimate directional change in species composition over time (Collins et al., 2000).

Third, we conducted a community weighted mean redundancy analysis (hereafter CWM-RDA; Kleyer et al., 2012) to examine the relationship between environmental variables (site types, soil properties and habitat characteristics) and CWM trait values of communities. We conducted a detailed analysis of those environmental variables using a subset of the wellsites and neighboring reference sites data (N = 60) that had all the covariates (soil properties sampled at different depths). In addition, we conducted the same analysis by including all sites (N = 89) and using the set of variables that were measured also in the young harvested sites from the ABMI core sites. To determine the link between each trait and each environmental variable, we performed a fourth-corner analysis (Legendre et al., 1997; Dray and Legendre, 2008). The fourth-corner tests the link between each species trait (Matrix Q: species x traits) and environmental variable (Matrix R: sites x environment) by way of species data (Matrix L: sites x species abundance). The significance (alpha = 0.05) of trait-environment links was tested by permutating the data based on a null model. Specifically, we applied a null model that shuffled species abundance independently, but with the constraint that it kept site species richness and total site abundances as observed. In addition, the null model kept species incidences as in the observed data. While total abundance of species in the randomized data was not strictly as observed, they were highly correlated (r = 0.96). For significance testing, we used 9999 permutations and the p-values were adjusted for multiple testing using the FDR method, which is appropriate and powerful method for addressing multiple testing issue in ecological studies (García, 2004; Verhoeven et al., 2005). We also considered a simple correlation between the CWM value for each trait and the continuous environmental variables to further corroborate the fourth corner results. Additionally, we assessed the change in CWM values for each individual trait with time since reclamation to highlight the shared and unique pattern underlying the trajectory based on overall CWM trait values.

In all analyses, rare species (singletons and doubletons) were removed prior to the analysis to alleviate potential effects of vagrant and hard to detect species on the overall relationship between traits and environmental variables. The fourth-corner analyses were conducted using fourthcorner function as implemented in the ade4 package for R (Dray and Dufour, 2007). All analyses were conducted in R, version 3.3.2 (R Core Team, 2017).

3. Results

3.1. Species richness and abundance

A total of 191 vascular plant species and two genera were included in our analysis. A summary of species richness and total relative abundance of all species averaged by site type is presented in Table 2. Species richness differed by site type (one-way ANOVA, $F_{4,84} = 5.69$, $p < 0.001$), with richness in young harvested sites (Y.Cut) higher than in young reclaimed (Y.Rec) sites (Tukey HSD, $p < 0.001$) (Table 2). The post-hoc pairwise comparisons indicated no significant difference in mean species richness across other site type pairs (Tukey HSD, all $p > 0.05$). Similarly, there was a significant difference in the total relative abundance for all species (i.e., detections of all species in 4 quadrants per site) among site types (one-way ANOVA, $F_{4,84} = 9.29$, $p < 0.001$), with total relative abundance in young harvested (Y.Cut) only higher than in young reclaimed (Y.Rec) and young forest (Y.For) site types (Table 2).

3.2. Differences in plant trait composition across site types

The PCA on CWM indicated that the first two axes explained 55.3% and 10.8% of trait co-variation, respectively (Fig. 1). The first axis had high positive loading for forbs, graminoids, short-lived, tall-stature,

Table 2
Vascular plant species richness summary statistics grouped by site type. Site types with significant difference (alpha = 0.05) based on one-way ANOVA post-hoc comparisons (Tukey HSD) are indicated by different capital letters (A, B).

Site type	Site code	No. sites	Number of species			Total Abundance		
			Total	Range	Mean ± S.D.	Total	Range	Mean ± S.D.
Young reclaimed	Y.Rec	18	134	17–58	40.7 ± 10.1^{B}	2028	35–149	112.7 ± 31.9^{B}
Old reclaimed	O.Rec	12	133	39–60	48.3 ± 6.5 ^{AB}	1622	99–167	135.2 ± 21.6 ^{AB}
Young harvested	Y.Cut	35	170	37–64	51.5 ± 7.6 ^{A}	5292	115–195	151.2 ± 20.4 ^{A}
Young forest	Y.For	7	126	43–62	49.7 ± 6.4 ^{AB}	801	101–132	114.4 ± 11.6^{B}
Mature forest	M.For	17	129	34–60	47.9 ± 6.9 ^{AB}	2278	94–183	134 ± 25.6 ^{AB}

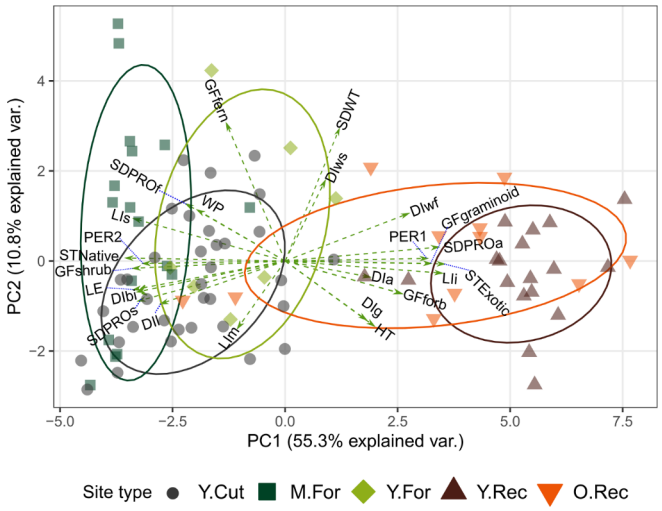

Fig. 1. Principal component analysis (PCA) of the Community Weighted Means (CWM) of 10 traits of understory plants assessed along a post-reclamation chronosequence and reference sites grouped by site type. Site type: Y.Rec = Young reclaimed; O.Rec = Old reclaimed; Y.Cut = Young harvested forest; Y.For = Young forest; M.For = Mature forest. Vectors indicate plant traits/characteristics. Refer to Table 1 for trait codes.

abundant seed production, far-dispersal by wind, light tolerance, and exotic species. In contrast, CWM for shrubs, perennials, increased lateral growth, production of few or scarce seed, dispersal by bird, insect or explosive, high moisture requirement, shade tolerance and native species had negative loading on the first axis. The first axis thus discriminated communities dominated by species with fast-resource acquisition traits (positive along x-axis) from those dominated by species with more "climax", resource-conservation traits (negative along x-axis). The traits that had strong positive links with the second axis were growth forms such as ferns and allies, short-wind dispersers and species that are shade tolerant and produce few large seeds (traits related to species typically found in later-successional habitats). The different site types showed an obvious trend along the first axis (positive to negative) from young reclaimed, old reclaimed, young harvested/young forest to mature forest. CWM trait composition of understory plant assemblages differed significantly between the site types (PERMANOVA, $F_{4,84} = 32.91$, $p < 0.001$), as was identified in the PCA plot. Despite the apparent overlap among reference site types in the PCA plot (e.g., harvested *vs* natural forests), post-hoc pairwise PERMANOVA tests indicated significant differences between all pairwise site-type comparisons (Table 3). Yet, the differences were much higher between reclaimed and reference sites than among the reference sites. There was a borderline significant difference in dispersion among site types (PERMDISP, $p = 0.048$) with dispersion for young harvested (Y.Cut) sites lower than for both young and old reclaimed wellsites (Y.Rec and O.Rec).

Table 3
Pairwise PERMANOVA tests of Community Weighted Mean traits for each pair of site types. P-values were adjusted for multiple testing using the false discovery rate method.

Site Type Comparison	F-value	R.squared	p
Y.Rec *vs* O.Rec	3.286	0.105	0.013
Y.Rec *vs* Y.Cut	95.842	0.653	0.001
Y.Rec *vs* Y.For	22.518	0.495	0.001
Y.Rec *vs* M.For	81.902	0.713	0.001
O.Rec *vs* Y.Cut	37.323	0.453	0.001
O.Rec *vs* Y.For	7.808	0.315	0.003
O.Rec *vs* M.For	34.444	0.561	0.001
Y.Cut *vs* Y.For	3.668	0.084	0.009
Y.Cut *vs* M.For	5.838	0.105	0.001
Y.For *vs* M.For	4.879	0.182	0.001

Y.Rec = Young reclaimed; O.Rec = Old reclaimed; Y.Cut = Young harvested site; Y.For = Young forest; M.For = Mature forest.

3.3. Directionality in community-level functional traits shift with reclamation age

The similarity in overall CWM trait composition between reclaimed wellsites and all of the reference site types (young harvested, young or mature natural forests) increased with post-reclamation age (Fig. 2; for individual trait trajectory see below). There was no significant difference in the trajectory slope towards the different reference site types, yet the intercept for young natural forest was higher than that of mature natural forest ($p = 0.002$). Furthermore, time-lag regression analysis indicated a directional change among the wellsites whereby the dissimilarity between wellsites increased with difference in time since reclamation between wellsite pairs (Fig. 3).

3.4. Community-level functional traits and environmental variables

The CWM-RDA indicated that the environmental variables explained 62.3% of the total variance in community traits (Fig. 4; Appendix Table S3). The first axis accounted for most (79.6%) of the CWM-RDA variance, with the second axis explaining 6.1%. Axis 1 represents a gradient of site types (Y.Rec to M.For), canopy closure (canopy; negative), coarse woody debris volume (CWD; negative), available organic matter at surface and deepest soil (OC_0 and OC_60; negative), surface bulk density (BD_0; positive), and pH (pH_0 and pH_60; positive). Traits associated with fast-resource acquisition (e.g., forbs, high dispersal, shade intolerant/light demanding, exotics) were positively correlated to Axis 1 and to variables that had positive loadings on Axis 1 such as bulk density (also see Fig. 1). In contrast, resource-conservation traits (e.g., shade tolerant, few seeds, and moisture preference) were negatively correlated with Axis 1; a pattern shared with variables such as canopy cover, coarse wood and mature forest that had negative loading on Axis 1. The second axis showed a weak relationship with pH, and traits including ferns, few seed production,

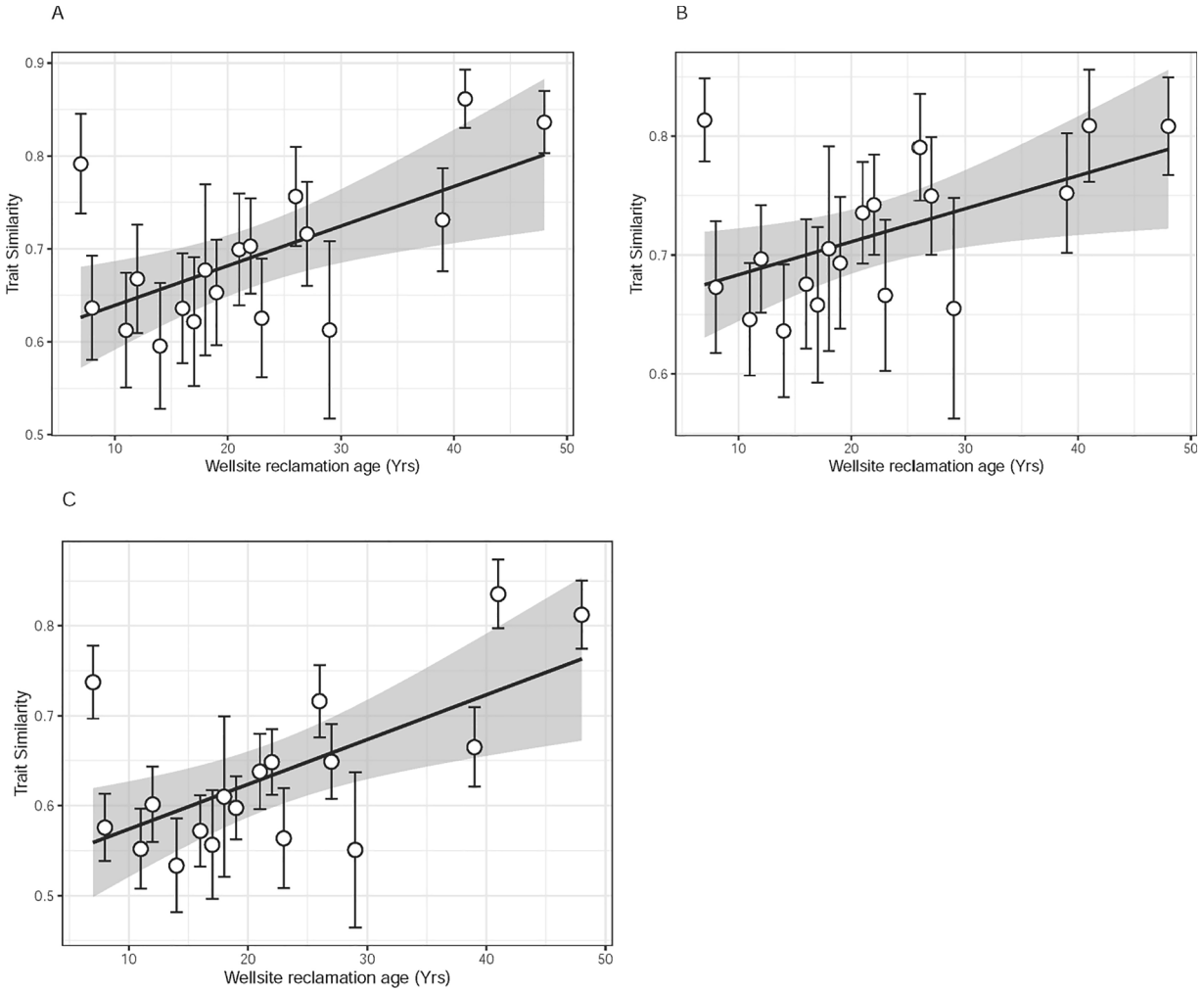

Fig. 2. Plot of trait composition similarity of reclaimed wellsites (based on CWM of traits and Gower metric) with time towards reference site types (A) Young harvested forest, (B) young and (C) mature natural forest. Gray shading shows 95% confidence interval of the correlation.

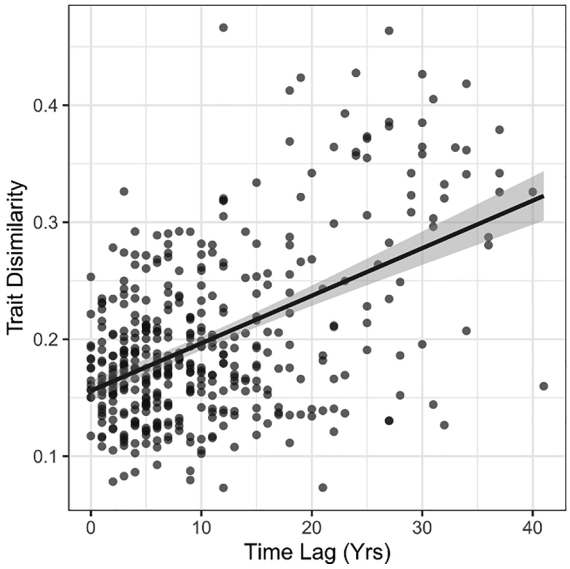

Fig. 3. Time-lag regression analysis showing increase in pairwise Gower dissimilarity in community-weighted trait means (CWM) trait composition (y-axis) between wellsite pairs with increasing time lags (age difference between wellsite pair; x-axis) among wellsite plant communities. Gray shading shows 95% confidence interval of the correlation.

and short-wind dispersers had negative loadings, whereas moderately shade tolerant had positive loading. Results of CWM-RDA analysis that included the complementary harvested site type data were qualitatively the same (Appendix Fig. S2).

Fourth-corner analysis using a fixed–fixed null model supported the contrasting relationship of those resource-acquisition and resource-conservation traits to the environmental variables observed in CWM-RDA (Fig. 5). Traits associated with fast resource acquisition positively correlated with reclaimed wellsites (Y.Rec and O.Rec) and associated variables, high bulk density and pH, but had negative association to mature forest (M.For), OC, CWD and canopy cover; the opposite relationship was found for resource-conservation traits. Young harvested (Y.Cut) and young naturally disturbed forest (Y.For) also shared some similarity as evidenced by a positive relationship with late-successional traits found in mature forest (e.g., shrubs, lateral extension, bird dispersed); yet many traits were non-significant (e.g., plant height, water preference and seed production). Additionally, some traits that initially had significant negative (seed production: few and scarce; dispersal mode: bird and limited) or positive (non-bird animal dispersed) associations with young reclaimed sites became non-significant over time in the old reclaimed sites, indicating gradual change in the abundance of these traits over time. Such gradual changes were more evident when considering the relationship between CWMs for individual traits and with time since reclamation of wellsites as a continuous variable (Table 4, Appendix Fig. S3). For example, CWM of traits such as graminoids, abundant seed production, far wind-dispersed, shade-

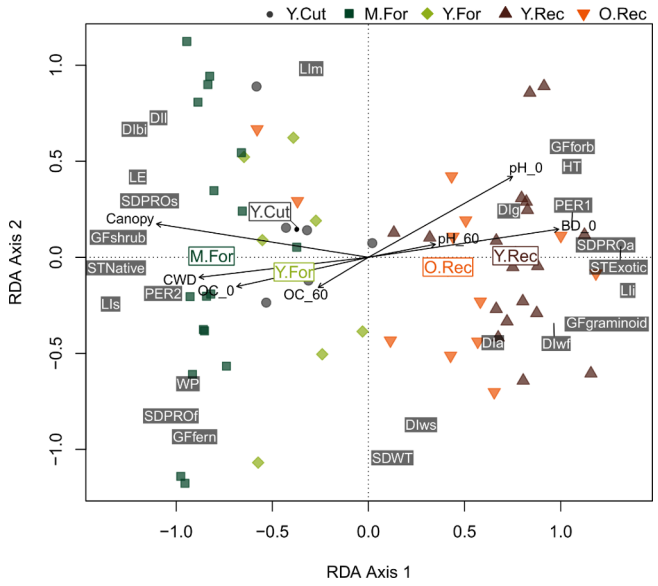

Fig. 4. Redundancy analysis (RDA) model in trait Community Weighted Mean. The first two axes explained 62.3% of the total CWM trait variance, of which 79.6% and 6.1% were explained in Axis-1 and Axis-2, respectively. Points are study sites, and site type centroids are indicated in boxed labels. Environmental variables are indicated by red arrow, and white text in grey boxes are short names for traits, which are explained in Table 1. Environmental variables are bulk density surface (BD_0), pH surface (pH_0), pH deep (pH_60), organic carbon surface (OC_0), organic carbon deep (OC_60), canopy cover (canopy) and coarse woody debris (CWD). Site codes as in Fig. 1.

intolerant (light-demanding) and non-native tended to decline with increasing reclamation age, while shrubs, few seed production, bird dispersers and shade tolerant traits tended to increase with time since reclamation, although not necessarily reaching the level found in the reference sites. Such trends over time were not always evident because of differences when comparing young and old reclaimed age classes. CWMs of traits of forbs, perenniality, height and water preference in wellsites remained consistently different from those of reference sites with no apparent trend with age of reclamation. Finally, for most of the examined traits, the refences site types were similar (also see Fig. 1); the limited difference observed in the overall trait composition among reference site types (Table 3) is probably due primarily to differences in CWM of just a few traits, including ferns (young harvested *vs.* mature forest) and graminoids (young forest *vs.* mature forest) (Appendix Fig. S3).

4. Discussion

Despite the sustained interest in ecological succession due to its pivotal role in understanding how plant communities respond to disturbance, the long-term successional trajectory of ecological communities' on severely degraded lands remains poorly understood (Dhar et al., 2018). In particular, far less is known about the recovery of functional composition of highly degraded lands following reclamation. Our study helps to fill this knowledge gap by evaluating the successional trajectory of plant community functional composition in reclaimed wellsites and effects of putative environmental variables on their recovery using long-term chronosequence data. We showed a general directional change of functional composition in reclaimed sites over time towards those found in reference sites (both natural origin and harvested), with some variation in successional trajectory among traits. Despite their overall similarity in terms of species richness and total relative abundance, the overall functional composition in reclaimed wellsites still differed from reference sites up to 50 years after reclamation. We found strong effects of environmental variables on overall functional composition as well as for individual traits.

A general directional successional change towards pre-disturbance community composition is a logical expectation under natural

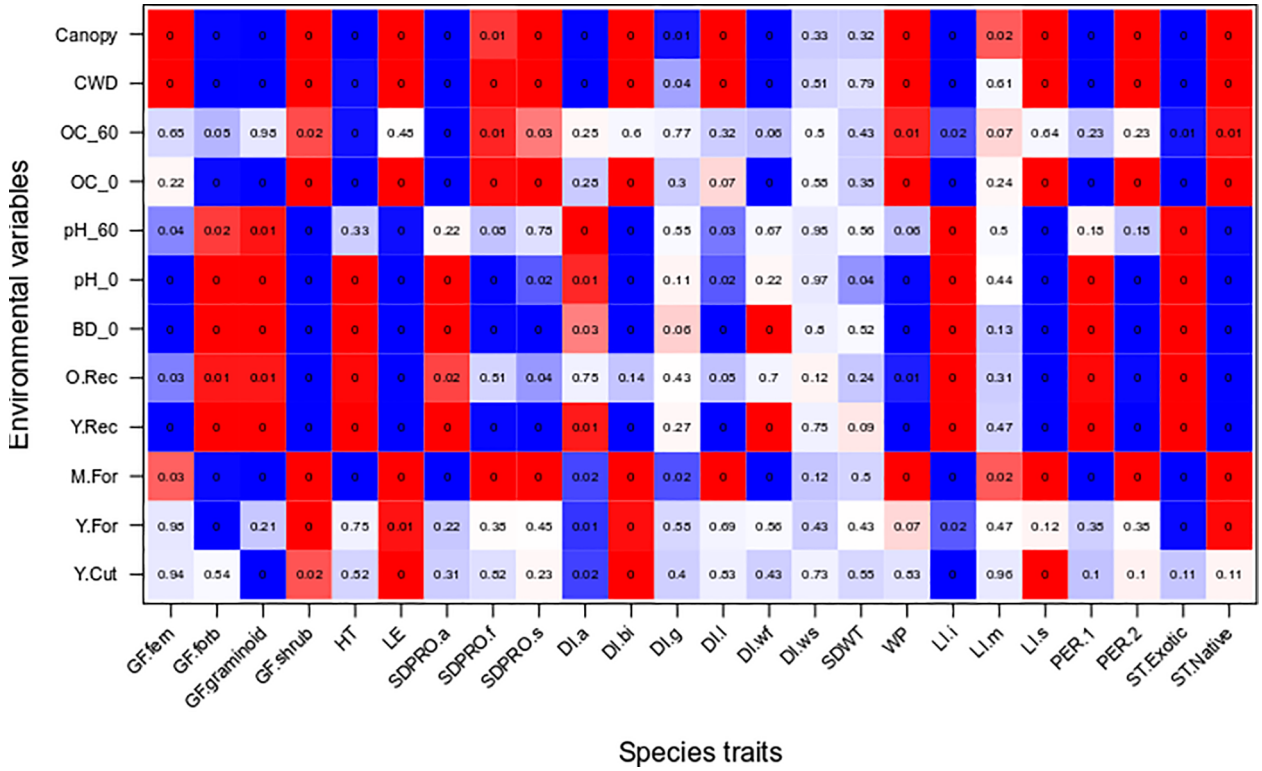

Fig. 5. Fourth corner analysis showing relationship between each pair of trait and environmental variables/site types. Significant positive and negative relationships are shown by red and blue color, respectively. Values are p-values. Abbreviations for traits are described in Table 1 and for environmental variables in Fig. 4.

Table 4
Summary of trajectory trend of community weighted mean (CWM) value for each trait with reclamation age (trend) towards that of reference site types.

Trait	Trait types	Trend	Similar as reference?	Remark: cwm in reclaimed
Growth form (GF)	Graminoid	↓	No	Higher than in reference
	Forb	NS	No	Higher than in reference
	Shrub	↑	No	Lower than in reference
	Fern	NS	Y.Cut	
Height (HT)	Continuous	NS	Y.Cut, Y.For	Higher than in M.For
Lateral extension (LE)	Ordinal	NS	No	Lower than in reference
Seed production (SDPRO)	Abundant (a)	↓	No	Higher than in reference
	Semi-abundant (s)	↑	Y.Cut, Y.For	Lower than in M.For
	Few, scarce (f)	↑	Y.For	Lower than in Y.Cut and M.For
Seed weight (SDWT)	Continuous	↓	Yes	Like that in reference regardless of age
Seed dispersal vector (DI)	Animal (a)	NS	M.For*	Higher than in Y.Cut and Y.For
	Bird (b)	↑	No	Lower than in reference
	Unassisted (g)	↓ns	Yes	Like that in reference
	Self-explosive, low (l)	↑	Y.For	Lower than in Y.Cut and M.For
	Wind far (wf)	↓	Yes	Like that in reference
	Wind short (ws)	NS	Yes	Like that in reference
Water preference (WP)	Ordinal	NS	Y.Cut, Y.For	Lower than in M.For
Light requirement (LI)	Shade intolerant (i)	↓	No	Higher than in reference
	Shade mid-tolerant (m)	NS	Yes	Like that in reference
	Shade tolerant (s)	↑	No	Lower than in reference
Longevity/perennially (PER)	Annual & biannual (1)	NS	No	Higher than in reference
	Perennial (2)	NS	No	Lower than in reference
Origin status (ST)	Exotic	↓	No	Higher than in reference
	Native	↑	No	Lower than in reference

Y.Rec = Young reclaimed; O.Rec = Old reclaimed; Y.Cut = Young harvested sites; Y.For = Young forest; M.For = Mature forest
The codes under "Trend" column indicate whether CWM values in reclaimed sites show increasing (↑), decreasing (↓) or no significant (NS) trend overtime. The values for reclaimed sites may be similar (reference site type indicated) or not (No) regardless of trend and this is indicated in "similar as reference" and "Remark" columns. For example, graminoid declined over time but still remained higher than reference sites, whereas fern did not show trend but values in reclaimed were similar to that found in young harvested. For detailed results see Appendix Fig. S3.

disturbance regimes that often leave substantial biotic and abiotic legacies (Turner et al., 1998; Roberts, 2004; Hart and Chen, 2006; Azeria et al., 2011). However, severe anthropogenic disturbances, such as energy development and mining projects, often create inhospitable biotic and abiotic conditions for site self-recovery, which require active reclamation practices to facilitate revegetation. Historically these practices have used non-native biotic communities (e.g., agronomic species) (Chazdon, 2008; Jones et al., 2018). These practices can create distinct ecological conditions which may further drive the successional trajectory of an ecosystem in a direction different from that observed after natural disturbances. Non-native species are known to have significant impacts on community assembly (Vilà et al., 2011; David et al., 2015). For example, novel soil physico-chemical condition and dense cover of non-native crops used in revegetation of coal sites have delayed succession by native vegetation (Zipper et al., 2011; Franklin et al., 2012; Bauman et al., 2015). These biological and environmental effects of disturbance and subsequent reclamation may be long lasting. Pinno and Hawkes (2015) found that the composition and structure of plant communities in reclaimed areas were still distinct from natural ecosystems after 20 years, while Lupardus et al. (2019) found that plant taxonomic composition left wellsites in a state of arrested succession for decades after reclamation. In contrast, our findings indicate a general directional change in mean trait values with increasing reclamation age and convergence towards reference sites. Yet, trait composition in reclaimed wellsites remained distinct from reference sites even after almost 50 years. Our results suggest there may be a consequence to the persistence of species with early-successional traits and exotic species that are better adapted to the novel soil conditions of reclaimed sites, preventing re-colonization of species with more desirable late-successional/performance traits.

The functional composition of young reclaimed sites (< 20 years) was dominated by characteristics of early-successional species such as light-demanding/shade-intolerant species, species that disperse effectively by wind, produce abundant seed and have short life span, as well as exotic species. This may reflect the selection of the species pool used for revegetation (i.e., "Introduction bias" sensu van Kleunen et al., 2015); species selected for revegetation are typically fast-growing and produce abundant seed so that soil stabilization is promoted (Cheivers et al., 2016). Historically, non-native species such as Timothy grass (*Phleum pratense*), alsike clover (*Trifolium hybridum*), red clover (*T. pratense*) and white clover (*T. repens*) as well as native species (e.g., slender wheatgrass *Agropyron trachycaulus*, fringed brome *Bromus ciliatus*) were widely used in active reclamation (e.g., Alberta Energy and Natural Resources, 1984; Hardy BBT Ltd., 1989; see Appendix Table S5 for non-native species). Furthermore, other functionally similar species including exotic (e.g., Canada thistle *Cirsium arvense* and common dandelion *Taraxacum officinale/erythrospermum*) and native (e.g., fireweed *Chamerion angustifolium*) invaders are well adapted to disperse and establish given the initial abiotic conditions (see below) and probably due to stochastic colonization processes; e.g., plants with abundant seeds would have higher probability of arriving and occupying in the short term (Hubbell, 2001; Duncan et al., 2009). In contrast, functional composition in older reclaimed sites tended to diverge from the typical early-successional syndrome and converge, albeit not completely, towards late-successional syndrome (e.g., increase in prevalence of species with shade-tolerance, produce fewer seeds, disperse via birds and prefer higher soil moisture conditions) found in reference sites. Thus, the post-reclamation assembly of communities appears to follow a predictable functional filtering (deterministic) process, whereby traits favored in the early successional (= fast resource acquisition traits/ colonization traits) stage are eventually replaced by late-successional traits (i.e., resource preservation traits/ performance traits). This is because most traits displayed a directional change and increased (e.g., semi-abundant seed) or decreased (e.g., abundant seed) over time reaching the reference level either partially (e.g., semi-abundant seed) or "fully" (e.g., far dispersal by wind). However, trajectories of traits such as forbs, lateral extension and perennials were poorly predicted by reclamation age, and they remained distinct from that of reference sites. On the other hand, traits such as short-dispersal wind and mid shade-tolerant of reclaimed sites were not different from

that of reference sites.

The above findings highlight the need to examine and understand how different traits individually and collectively contribute to the overall successional trajectory and potential ecosystem functions of severely degraded landscapes. For example, the lack or delayed trajectory of traits such as longevity, is likely to contribute to the apparent delayed recovery of reclaimed sites inferred from overall assemblage trait composition. This also highlights the need for careful consideration of the traits considered when using this approach to infer factors that influence recovery. Furthermore, the observed multiple trajectories by traits may highlight the shared and differential influence of underlying environmental drivers on traits during post-reclamation succession (see below).

Directional change, or lack thereof, in functional composition partially hinges on the trait-environment relationship. In this deterministic view of succession, species are selected from the regional species pool based on their functional attributes that confer fitness to the local environment (Helsen et al., 2012; Kraft et al., 2015; Weiher and Keddy, 1999). Our results provide strong evidence for effects of environmental filtering on trait composition along the post-reclamation successional and reference gradients (but with some exceptions highlighted in the paragraph directly below). We found a strong relationship between CWMs of traits and local soil physico-chemical properties and habitat variables. High soil bulk density and pH as well as the low amount of total organic carbon, coarse woody debris and canopy cover in young reclaimed wellsites favored fast-resource acquisition traits including abundant seed, far-wind dispersed, taller plants, short life span, shade-intolerant, graminoids, forbs and exotics. The opposite was true for trait composition in reference sites and to some extent in old reclaimed wellsites in which traits typical of late successional and/or resource-conserving species became more abundant, including scarce seed production, dispersal via birds, perennials, shade-tolerant, water-preferring, extensive lateral extension, shrubs and natives. Canopy cover increased with time since reclamation and certain traits showed a concurrent directional decline (e.g., graminoid, abundant seed and wind-far dispersed, shade-intolerant) or increase (e.g., bird dispersed and shade-tolerant). This suggests environmental filtering acted as a major driver of community assembly as trait composition shifted towards those associated with later-successional habitats. Other traits however did not appear to follow a directional change along a post-reclamation chronosequence, including traits such as forbs, root lateral extension and life-span. These traits were still associated with soil physico-chemical and other attributes that remained consistently high (bulk density and pH) or low (OC and CWD) along our post-reclamation chronosequence. For instance, root lateral spread was negatively related to bulk density and pH and the converse was true for forbs; both traits remained consistently low or high along the chronosequence. Thus, the absence of a successional trajectory in these traits could be due to contingent factors such as soil physico-chemical attributes rather than stochastic factors, as discussed below.

Our findings also showed some traits were similar across well sites and reference sites with no strong signal regarding the effect of site, environmental variables or time since reclamation. For example, we did not find significant difference of the shade mid-tolerant with age since reclamation unlike the decline and increase observed for shade-intolerant/light demanding and shade-tolerant, respectively. It is generally assumed that as an ecosystem develops the assemblage will reflect species with different light requirements and the gradual replacement of shade-intolerant species by mid-tolerant and finally shade-tolerant ones. The lack of significant difference for mid-tolerant species may be because such species are often generalists and perform equally well along the entire light gradient in the study system. Similarly, short-distance wind dispersers did not show any evident relationship with respect to site types, age since reclamation or any of the variables examined (Appendix Fig. S3 and Fig. S3) unlike other dispersal classes, e.g., far-dispersal by wind. The reason for this was not obvious from our data. The most abundant short-distance wind dispersers in our study are ubiquitous graminoids and herbs (*Calamagrostis canadensis, Achillea millefolium* and *Mertensia paniculata*), similar to the shade mid-tolerant species, they are known to thrive well in a wide variety of site conditions.

The persistence of graminoids (including exotic agronomic species that were initially seeded), forbs, and annuals as well as high bulk density and pH for soil conditions in reclaimed sites highlight the long-term legacy effects that intensive disturbance and the type of species used in reclamation can leave on the landscape. Collectively, these factors can severely delay the establishment of native biota for decades (Zipper et al., 2011; Franklin et al., 2012). Herbaceous annuals used in reclamation may inhibit or delay the successional trajectory through direct competition (Zipper et al., 2011), priority effects (Fukami et al., 2005; Kardol et al., 2013) or through apparent competition by attracting browsers (Holt and Lawton, 1994). Our data indicate that animal dispersed traits are more common in young reclaimed sites than in reference sites, which may also suggest herbivore use of the reclaimed sites. Browsing intensity has been documented to favour the development of a herbaceous layer (Rooney, 2009). Similarly, exotic species are widely recognized to impact structure and composition of native biota, and succession dynamics, directly through biotic interactions or indirectly through modification of soil physico-chemical properties (Vilà et al., 2011). The persistence of exotic species used for reclamation and other functionally similar invading exotics in reclaimed sites in our study highlights their potential long-term impact on community succession (David et al., 2015). Consideration of such potential biotic effects may further our understanding of succession dynamics of reclaimed sites. Taken together, our results provide empirical evidence for the importance of temporal and environmental filters, as well as potentially for biotic interactions in shaping community assembly and recovery of severely disturbed forest ecosystems following oil and gas disturbance and subsequent reclamation.

We recognize there are potential limitations to our inference regarding the temporal effect based on the assumption that reclaimed sites had identical biotic and abiotic starting conditions. One such limitation is the time since certification does not account for possible passive regeneration that may have occurred prior to reclamation and for different amounts of time that a wellsite may have been reclaimed prior to applying for a reclamation certificate. In addition, there is variation in how practitioners may have implemented the reclamation criteria – for example there could be some variation in the application of the recommended seed mixes (Alberta Energy and Natural Resources, Forest Service, 1984). In our study, we noted a few reclaimed sites deviated from the general pattern of successional trend over time, either faster or slower, which may suggest such site-specific local- or landscape factors and possibly historical contingency related to restoration practices (Young et al., 2005). However, despite such potential limitations, our findings provide strong evidence of directional temporal change of functional composition of highly degraded lands following reclamation. Our study has demonstrated the value of using a trait-based approach in deciphering generalized patterns beyond differences in species identity and geographical extent (e.g., Diaz et al., 2004; McGill et al., 2006).

Our results contribute to a mechanistic understanding of ecological succession following reclamation that may inform restoration/reclamation practices. Certain biotic and abiotic conditions inhibited the functional recovery towards natural or other desired targets. As shown by other studies (e.g., Zipper et al., 2011; David et al., 2015) we detected persistence of early successional, exotic species and/or herbaceous species used for revegetation, which may inhibit the establishment of native species from the regional species pool. In the studied region (Alberta), reclamation criteria have already been updated to restrict the use of exotic grasses and forbs with fast resource acquisition traits (e.g., abundant seed production and annuals) and instead promote the use of natives with similar attributes for revegetation. Indeed, the current

reclamation criteria recognize that competitive herbaceous species may inhibit development of natural forest biota trajectory and that development of shrubs should be encouraged (ESRD, 2013). In addition, the persistence of undesired plants in reclaimed wellsites could be due to enduring novel soil physico-chemical properties, notably high bulk density and pH, which also appear to inhibit establishment of shrubs and other late-stage successional species. Measures to alleviate soil compaction by tilling may enhance shrubs and other late-successional species (e.g., with extensive root lateral extension). Certainly, there is a need to re-develop other natural attributes such as soil carbon content and coarse woody debris on these wellsites, which could be more complex and take a much longer time to recover (Brown et al., 2003). Indeed, the presence of such biological legacies and seed banks are key elements that distinguish natural disturbances from more severe soil-modifying anthropogenic disturbances, and which play a significant role in accelerating ecosystem recovery (Turner et al., 1998; Roberts, 2004; Hart and Chen, 2006; Dhar et al., 2018). Similarly, forestry timber harvest and silvicultural practices often leave a significant proportion of the biological legacies on site and retain some mature standing trees, as in the harvested sites included in our study (Johnstone et al., 2016). Although our study was not designed to specifically examine the post-harvest recovery, the overall similarity of those young harvested sites with young and mature naturally disturbed forests in our study may be linked to the forest floor and canopy cover legacy facilitating recovery. The importance of canopy cover for restoration of understory vegetation is highlighted also by our finding that linked directional change to canopy development. Overstory cover and composition can affect nutrient availability and microclimate attributes and consequently the understory community assembly and composition (Bartemucci et al., 2005; Hart and Chen, 2006; Barbier et al., 2008; Azeria et al., 2011). Therefore, newer reclamation criteria that include planting or seeding trees and shrubs to enhance canopy cover development can be an effective reclamation/restoration approach to encourage longer-term establishment of late-successional species with associated trait syndromes (Holl, 2002; Chen et al., 2017).

Understanding the functional recovery of highly anthropogenically-disturbed ecosystems that are degraded beyond natural disturbance analogues is vital to evaluate how they compare with the generality of successional dynamics findings from studies in naturally disturbed areas, along with those that have intermediate anthropogenic disturbance levels (e.g., conventional harvesting). Our study provides empirical evidence for a directional yet slow change of functional composition of understory plants in severely disturbed forested ecosystems following reclamation, and identifies important trait-environmental relationships driving the successional trajectory we found here. Our findings have important implications for future restoration and reclamation efforts as they provide a more mechanistic understanding for what has often been observed to be a slow recovery in reclaimed wellsites. Further studies are required to establish the generality and relevance of these findings for improving reclamation efforts, such as by providing guidance in selecting species with traits that best perform under certain environmental conditions (e.g., Martínez-Garza et al., 2013) or modifying those limiting conditions to enhance establishment of desired species (e.g., Lohbeck et al., 2017). When the relationship between traits and ecosystem functions can be established, such an approach could also have important implications on measures of ecosystem function recovery and reclamation policies requirements such as “equivalent land capability” (Alberta Environment, 2010; ESRD, 2013). A trait-based approach may be promising to refine the assessment and forecasting of the long-term recovery of severely disturbed land after reclamation. It may provide a generalizable framework to compare successional trajectories of landscapes impacted by various natural and anthropogenic disturbance agents that leave differing levels of biological legacies.

CRediT authorship contribution statement

Ermias T. Azeria: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing - original draft, Writing - review & editing. **Kierann Santala:** Conceptualization, Methodology, Investigation, Validation, Writing - review & editing. **Anne C.S. McIntosh:** Conceptualization, Data curation, Investigation, Methodology, Project administration, Validation, Writing - review & editing. **Isabelle Aubin:** Conceptualization, Methodology, Investigation, Project administration, Validation, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We want to start by acknowledging Arnold Janz’s foundational contributions to this work, without which the preparation of this manuscript would not have been possible. Arnold developed the concept of the Ecological Recovery Monitoring program (ERMP) in 2003 and has lobbied for program support since then. He collaborated with ERMP to develop forest well pad sampling protocols; these protocols and ERMP data on the 60 sites collected in 2014 were essential for the current manuscript. We appreciate the contributions of the ERMP Advisory Group members – especially Dan Farr. Thanks to Kellina Higgins for assistance in surveying literature on traits and to Laura Boisvert-Marsh for trait data management and English Edition. Financial support was provided by the Office of Energy Research and Development, Natural Resources Canada, Canada. Core field research team members for data collection at the 30 wellsites and adjacent reference sites included Lee-Ann Bauman (Nelson), Victor Bachmann, Elise Martin, Andrew Underwood, Carissa Wasyliw, and Scott Wilson. The ecological recovery monitoring project that collected the data for the 30 wellsites and adjacent reference sites was initiated and funded by Alberta Environment and Sustainable Resource Development’s Land Monitoring Team, Canada to Alberta Biodiversity Monitoring Institute, Canada (ABMI) (AESRD 2012-2015), then to ABMI from the Alberta Environmental Monitoring Evaluation and Reporting Agency (AEMERA 2015-16), and most recently with Environmental Monitoring & Science Division, Alberta Environment and Parks, Canada (AEP 2017-20) funding to A McIntosh (AE 18GRAEM04 and 05 McIntosh). The project has also been supported by the Alberta Biodiversity Monitoring Institute Application Centre and Alberta Innovates - Technology Futures, Canada (AITF - now Innotech Alberta) and Energy Innovation Program (Natural Resources Canada).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118180.

References

Aide, T.M., Zimerman, J.K., Pascarella, J.B., Rivera, L.W., Humfredo, M.-V., 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Rest. Ecol. 8, 328–338.

Alberta Biodiversity Monitoring Institute (ABMI) 2010. Terrestrial field data collection protocols (10001), Version 2010-04-20. Edmonton: ABMI.

Alberta Energy and Natural Resources, Forest Service. 1984. The resource handbook: operation guidelines for industry, 66 pp. Available online at: https://archive.org/details/resourcehandbook00albe.

Alberta Energy Regulator, 2019. ST37: List of Wells in Alberta. http://www1.aer.ca/ProductCatalogue/10.html (accessed 20 July 2019).

Alberta Environment 2010. Guidelines for Reclamation to Forest Vegetation in the

Athabasca Oil Sands Region, 2nd ed.; Prepared by the Terrestrial Subgroup of the Reclamation Working Group of the Cumulative Environmental Management Association: Fort McMurray, AB, Canada.
Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. 9, 683–693.
Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.
Aubin, I., Cardou, F., Boisvert-Marsh, L., Garnier, E., Strukelj, M., Munson, A.D., 2020. Managing data locally to answer questions globally: the role of collaborative science in ecology.". J. Veg. Sci. 31, 509–517. https://doi.org/10.1111/jvs.12864.
Azeria, E.T., Bouchard, M., Pothier, D., Fortin, D., Hébert, C., 2011. Using biodiversity deconstruction to disentangle assembly and diversity dynamics of understorey plants along post-fire succession in boreal forest. Glob. Ecol. and Biog. 20, 119–133.
Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanism involved- A critical review for temperate and boreal forests. For. Ecol. Manage. 254, 1–15.
Bartemucci, P., Messier, C., Canham, C.D., 2005. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forest of Quebec. Can. J. For. Res. 36, 2065–2079.
Bauman, J.M., Cochran, C., Chapman, J., Gilland, K., 2015. Plant community development following restoration treatments on a legacy reclaimed mine site. Ecol. Engin. 83, 521–528.
Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc. 57, 289–300.
Brown, R.W., Amacher, M.C., Mueggler, W.F., Kotuby-Amacher, J. 2003. Re-establishing natural succession on acidic mine spoils at high elevation: Long-term ecological restoration, Ogden, UT: USDA Forest Service. (USDA Forest Service Research Paper RMRS-RP-41).
Chazdon, R.L., 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320, 1458–1460.
Chen, H.Y.H., Biswas, S.R., Sobey, T.M., Brassard, B.W., Bartels, S.F., 2017. Reclamation strategies for mined forest soils and overstory drive understory vegetation. J. Appl. Ecol. 55, 926–936.
Chivers, I.H., Jones, T.A., Broadhurst, L.M., Mott, I.W., Larson, S.R., 2016. The merits of artificial selection for the development of restoration-ready plant materials of native perennial grasses. Rest. Ecol. 24, 174–183.
Collins, S.L., Micheli, F., Hartt, L., 2000. A method to determine rates and patterns of variability in ecological communities. Oikos 91, 285–293.
Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The Amer. Nat. 111, 1119–1144.
D'Astous, A., Poulin, M., Aubin, I., Rochefort, L., 2013. Using functional diversity as an indicator of restoration success of a cut-over bog. Ecol. Eng. 61, 519–526.
David, A.S., Zarnetske, P.L., Hacker, S.D., Ruggiero, P., Biel, R.G., Seabloom, E.W., 2015. Invasive Congeners Differ in Successional Impacts across Space and Time. PLoS ONE 10, e0117283. https://doi.org/10.1371/journal.pone.0117283.
de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., et al., 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. Biod. Cons. 19, 2873–2893.
Dhar, A., Comeau, P.G., Karst, J., Pinno, B.D., Chang, S.X., Naeth, M.A., Vassov, R., Bampfylde, C., 2018. Plant community development following reclamation of oil sands mine sites in the boreal forest: a review. Envi. Rev. 26, 286–298.
Díaz, S., Cabido, M., Casanoves, F., 1998. Plant functional traits and environmental filters at a regional scale. J. Veget. Sci. 9, 113–122.
Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., et al., 2004. The plant traits that drive ecosystems: Evidence from three continents. J. Veget. Sci. 15, 293–304.
Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G., et al., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46.
Drake, J.A., 1990. The mechanics of community assembly and succession. J. Theor. Biol. 147, 213–233.
Dray, S., Dufour, A., 2007. The ade4 package: Implementing the duality diagram for ecologists. Journal of Statistical Software 22, 1–20.
Dray, S., Legendre, P., 2008. Testing the species traits-environment relationships: the fourth-corner problem revisited. Ecology 89, 3400–3412.
Duncan, R.P., Diez, J.M., Sullivan, J.J., Wangen, S., Miller, A.L., 2009. Safe sites, seed supply, and the recruitment function in plant populations. Ecology 90, 2129–2138.
Environment and Sustainable Resource Development (ESRD). 2013. 2010 Reclamation Criteria for Wellsites and Associated Facilities for Forested Lands (Updated July 2013). Edmonton, Alberta. 81 pp. Available at: https://open.alberta.ca/dataset/9780778589846.
Franklin, J.A., Zipper, C.E., Burger, J.A., Skousen, J.G., Jacobs, D.F., 2012. Influence of herbaceous ground cover on forest restoration of eastern US coal surface mines. New Forest. 43, 905–924.
Fukami, T, Bezemer, T.M., Mortimer, S.R., van der Putten, W.H., 2005. Species divergence and trait convergence in experimental plant community assembly. Ecol. Lett. 8, 1283–1290.
Funk, J.L., Larson, J.E., Ames, G.M., Butterfield, B.J., Cavender-Bares, J., Firn, J., et al., 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biol. Rev. Camb. Philos. Soc. 92, 1156–1173.
García, L.V., 2004. Escaping the Bonferroni iron claw in ecological studies. Oikos 105, 657–663.
Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., et al., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637.
Government of Alberta. 1995. Reclamation criteria for wellsites and associated facilities: 1995 update. Edmonton, Alberta. pp. 62. Available at: https://open.alberta.ca/publications/9780778589853 (Accessed July 2019).
Gondard, H., Jauffret, S., Aronson, J., Lavorel, S., 2003. Plant functional types: a promising tool for management and restoration of degraded lands. Appl. Veget. Sci. 6, 223–234.
Gower, J.C., 1971. A general coefficient of similarity and some of its properties. Biometrics 27, 857–874.
Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., 1997. Integrated screening validates primary axes of specialization in plants. Oikos 79, 259–281.
Grime, J.P., 1977. Evidence for existence of 3 primary strategies in plant and its relevance to ecological and evolutionary theory. American Nat. 111, 1169–1194.
Hardy BBT Ltd., 1989. Manual of plant species suitability for Reclamation in Alberta, 2nd ed. Alberta Land Conservation and Reclamation Council Report No. RRTAC 89-4. pp. 436. https://doi.org/10.7939/R3FW17.
Hart, S.A., Chen, H.Y.H., 2006. Understory vegetation dynamics of North American boreal forests. Crit. Rev. in Plant Sci. 25, 381–397.
Helsen, K., Hermy, M., Honnay, O., 2012. Trait but not species convergence during plant community assembly in restored semi-natural grasslands. Oikos 121, 2121–2130.
Hiers, J.K., Mitchell, R.J., Barnett, A., Walters, J.R., Mack, M., Williams, B., Sutter, R., 2012. The dynamic reference concept: Measuring restoration success in a rapidly changing no-analogue future. Ecol. Rest. 30, 27–36.
Hobbs, R.J., Norton, D.A., 1996. Towards a conceptual framework for restoration ecology. Rest. Ecol. 4, 93–110.
Holl, K.D., 2002. Long-term vegetation recovery on reclaimed coal surface mines in the eastern USA. J. Appl. Ecol. 39, 960–970.
Holt, R.D., Lawton, J.H., 1994. The ecological consequences of shared natural enemies. Annu. Rev. Ecol. Syst. 25, 495–520.
Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, New Jersey, USA.
Huggard, D.J., Grover, B.E., Dzus, E., Smith, M., Schieck, J., 2015. Effectiveness monitoring for biodiversity: comparing 15 year old structural retention harvest areas to fires in boreal aspen. Can. J. Fores. Res. 45, 153–161.
Huston, M., Smith, T., 1987. Plant succession: life history and competition. Amer. Nat. 130, 168–198.
Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L.W., Schoennagel, T., Turner, M.G., 2016. Changing disturbance regimes, ecological memory, and forest resilience. Front. Ecol. Environ. 14 (7), 369–377.
Jones, C.E., Bachmann, S., Lieffers, V.J., Landhäusser, S.M., 2018. Rapid understory plant recovery following forest floor protection on temporary drilling pads. Rest. Ecol. 26, 48–55.
Kardol, P., Souza, L., Classen, A.T., 2013. Resource availability mediates the importance of priority effects in plant community assembly and ecosystem function. Oikos 122, 84–94.
Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. J. Veget. Sci. 3, 157–164.
Kleyer, M., Dray, S., de Bello, F., Leps, J., Pakeman, R.J., Strauss, B., et al., 2012. Assessing species and community functional responses to environmental gradients: which multivariate methods? J. Veget. Sci. 23, 805–821.
Kraft, N.J., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. Func. Eco. 29, 592–599.
Kumordzi, B.B., Bello, F., Freschet, G.T., Bagousse-Pinguet, L., Lepš, J., Wardle, D.A., 2015. Linkage of plant trait space to successional age and species richness in boreal forest understorey vegetation. J. Ecol. 103, 1610–1620.
Laughlin, D.C., 2014. Applying trait-based models to achieve functional targets for theory-driven ecological restoration. Ecol. Lett. 17, 771–784.
Lavorel, S., Garnier, E., 2002. Predicting the effects of environmental changes on plant community composition and ecosystem functioning: revisiting the Holy Grail. Funct. Ecol. 16, 545–556.
Legendre, P., Galzin, R., Harmelin-Vivien, M., 1997. Relating behavior to habitat: solutions to the fourth-corner problem. Ecology 78, 547–562.
Lohbeck, M., Winowiecki, L., Aynekulu, E., Okia, C., Vågen, T., 2017. Trait-based approaches for guiding the restoration of degraded agricultural landscapes in East Africa. J. Appl. Ecol. 55, 59–68.
Lupardus, R., McIntosh, A.C.S., Janz, A., Farr, D., 2019. Succession after reclamation: Identifying and assessing ecological indicators of forest recovery on reclaimed oil and natural gas well pads. Ecol. Indic. 106. https://doi.org/10.1016/j.ecolind.2019.105515.
Lupardus, R.C., Azeria, E.T., Santala, K., Aubin, I., McIntosh, A.C.S., 2020. Uncovering traits in recovering grasslands: A functional assessment of oil and gas well pad reclamation. Ecol. Eng. https://doi.org/10.1016/j.ecoena.2019.100016.
Macdonald, S.E., Quideau, S.A., Landhäusser, S.M., 2012. Rebuilding boreal forest ecosystems after industrial disturbance. In: Vitt, D., Bhattia, J. (Eds.), Restoration and reclamation of boreal ecosystems. Cambridge University Press, New York, pp. 123–160.
Martínez-Garza, C., Bongers, F., Poorter, L., 2013. Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? For. Ecol. Manage. 303, 35–45.
McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185.
McIntosh, A.C.S., Drozdowski, B., Degenhardt, D., Powter, C.G., Small, C.C., Begg, J., Farr, D., Janz, A., Lupardus, R.C., Ryerson, D., Schieck, J., 2019. Monitoring ecological recovery of reclaimed wellsites: protocols for quantifying recovery on forested lands. MethodsX 6, 876–909.
Meiners, S.J., Cadotte, M.W., Fridley, J.D., Pickett, S.T., Walker, L.R., 2015. Is

successional research nearing its climax? New approaches for understanding dynamic communities. Funct. Ecol. 29, 154–164.
Naeem, S., Duffy, J.E., Zavaleta, E., 2012. The functions of biological diversity in an age of extinction. Science 336, 1401–1406.
Natural Regions Committee 2006. Natural Regions and Subregions of Alberta. Compiled by Downing, D.J., Pettapiece, W.W. Government of Alberta. Pub. No. T/852.
Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., Daniel, H., 2009. On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. Oikos 118, 391–402.
Pickett, S.T.A., Collins, S.L., Armesto, J.J., 1987. Models, mechanisms and pathways of succession. Bot. Rev. 53, 335–371.
Pinno, B., Hawkes, V., 2015. Temporal trends of ecosystem development on different site types in reclaimed boreal forests. Forests 6, 2109–2124.
Powter, C.B., Chymko, N.R., Dinwoodie, G., et al., 2012. Regulatory history of Alberta's industrial land conservation and reclamation program. Can. J. Soil Sci. 92, 39–51.
Purcell, A.H., Friedrich, C., Resh, V.H., 2002. An assessment of a small urban stream restoration project in northern California. Rest. Ecol. 10, 685–694.
R-Core Team 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
Reich, P.B., 2014. The world-wide "fast-slow" plant economics spectrum: a traits manifesto. J. Ecol. 102, 275–301.
Remaury, A., Guittonny, M., Rickson, J., 2018. The effect of tree planting density on the relative development of weeds and hybrid poplars on revegetated mine slopes vulnerable to erosion. New Forest. 50, 1–18.
Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. Can. J. Bot. 82, 1273–1283.
Rooney, T.P., 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecol. 202, 103–111.
Ruiz-Jaen, M.C., Aide, T.M., 2005. Restoration success: how is it being measured? Rest. Ecol. 13, 569–577.
Schoenholtz, S.H., Van Miegroet, H., Burger, J.A., 2000. A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities. For. Ecol. Manage. 138, 335–356.
Schuster, M.J., Wragg, P.D., Reich, P.B., 2018. Using revegetation to suppress invasive plants in grasslands and forests. J. Appl. Ecol. 55, 2362–2373.
Thuiller, W., Richardson, D., Rouget, M., Proches, S., Wilson, J., 2006. Interactions between environment, species traits, and human uses describe patterns of plant invasions. Ecology 87, 1755–1769.
Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1, 511–523.
van Kleunen, M., Dawson, W., Maurel, N., 2015. Characteristics of successful alien plants. Mol. Ecol. 24, 1954–1968.
Verhoeven, K.J.F., Simonsen, K.L., McIntyre, L.M., 2005. Implementing false discovery rate control: increasing your power. Oikos 108, 643–647.
Vilà, M., Espinar, J.L., Hejda, M., et al., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol. Let. 14, 702–708.
Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional!. Oikos 116, 882–892.
Weiher, E., Keddy, P.A., 1999. Assembly rules as general constraints on community composition. In: Weiher, E., Keddy, P.A. (Eds.), Ecological assembly rules; perspectives, advances, retreats. Cambridge University Press, Cambridge, pp. 257–271.
Wortley, L., Hero, J.M., Howes, M., 2013. Evaluating ecological restoration success: a review of the literature. Rest. Ecol. 21, 537–543.
Young, T.P., Petersen, D.A., Clary, J.J., 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. Ecol. Let. 8, 662–673.
Zipper, C.E., Burger, J.A., Skousen, J.G., Angel, P.N., Barton, D., Davis, V., Franklin, J.A., 2011. Restoring forests and associated ecosystem services on Appalachian coal surface mines. Envir. Manag. 47, 751–765.